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Review

Plant growth regulators for enhancing revegetation success in reclamation: A review

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ABSTRACT

Plant growth regulators (PGRs) are natural hormones and synthetic hormone analogues. Types of PGRs reviewed in this paper include auxins, gibberellins, cytokinins, ethylene, abscisic acid, brassinosteroids and jasmonates. At low concentrations, PGRs have the capacity to influence cell division, cell expansion, and cell structure and function, in addition to mediating environmental stress. The direct application to plant roots, shoots, leaves, buds and flowers has been shown to increase resilience to abiotic and biotic stress, break seed dormancy, improve drought tolerance and water use efficiency, improve temperature tolerance, improve nitrogen use efficiency, promote shoot elongation and generation, increase shoot and root mass, stimulate root growth and lateral root development, and promote photosynthesis. PGR products are commonly used throughout agriculture, viticulture, and horticulture to improve plant growth and crop yield under non-ideal soil and environmental conditions. PGR products have yet to be trialed and registered for reclamation purposes in Canada. Their use may improve reclamation success by enhancing growth of slow-growing native plants and transplanted seedlings and cuttings; promoting the redevelopment of soil bacterial communities (including rhizobacteria); enhancing plant growth under environmentally stressful conditions; and, increasing adaptation and resiliency during climate change. There are significant opportunities for seed development, plant propagation and bioengineering in North America for both greenhouse-based and field-based applications. If successful, PGR use on native plants may improve the ecological function of disturbed lands by reducing the timeframe for reclamation and facilitating the achievement of reclamation end goals.

1. Introduction

1.1. Plant hormones and plant growth regulators (PGRs)

All plants naturally produce hormones that regulate metabolism, growth and development (i.e., plant shape, size and function) in response to their surrounding environment. Hormones (or chemical messengers) are produced in a variety of locations (i.e., buds, leaves, roots), and are moved throughout the plant system until they bind to receptors and trigger responses in targeted cells (Mitchell, 1942; Rademacher, 2015). Hormones influence cell division (cell number), cell expansion (cell size), and cell structure and function (cell differentiation), and have the capacity to control how a plant responds to environmental stress (Ferguson and Grafton-Cardwell, 2014). They can have multiple effects and elicit different responses depending on the target cells/tissues, developmental stage of the plant, concentration relative to other hormones, nutrient and water availability, uptake and storage, and climate/environmental conditions (Ferguson and Grafton-Cardwell, 2014).

There are a small number of hormones with the capacity to regulate plant physiological processes (Ferguson and Grafton-Cardwell, 2014) that have been studied since the 1930's for improving crop development and production (Rademacher, 2015). These hormones exist in low concentrations within plant tissue, resulting in large challenges in isolation, identification and extraction of suitable quantities for laboratory testing (Rademacher, 2015). By applying synthetic hormones, one can control similar processes, such as the formation and growth of roots, shoots, buds, flowers and fruits (Flasinski and Hac-Wydro, 2014). This finding resulted in the commercial production of synthetic hormone products, also termed plant growth regulators (PGRs).

PGRs have been measured to beneficially improve plant germination, growth and development by modifying hormonal activity within a plant (Harms and Oplinger, 1988; Hopkins and Hüner, 2004). The factors that control plant growth behaviour in response to PGRs include the type of plant, type of stimulant, amount of stimulant applied, timing of application, stage of growth, and location of stimulant application

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(Mitchell, 1942).

PGRs have been commonly used throughout agriculture, viticulture and horticulture to improve growth under non-ideal or stressful conditions (e.g., low soil fertility, disease, short growing seasons) (Mitchell, 1942; Rademacher, 2015; Weintraub and Norman, 1949), and to increase crop yield and ease of crop harvest (e.g., preventing pre-harvest fruit drop, hastening maturity and ripening, etc.) (Harms and Oplinger, 1988).

1.2. Land reclamation challenges

Both natural (e.g., forest fires, pests) and anthropogenic (e.g., resource extraction, construction, etc.) land disturbances are common across all landscapes, representing major forms of environmental stress for re-establishing plant communities. Land reclamation is the return of lands disturbed by industrial development to a natural or useful state. Reconstructed environments following disturbance are often associated with plant stress owing to a lack of nutrients, lack of topsoil, soil admixing, re-establishment of moisture, etc.

The climate has been measured to have undergone a warming over the last century (Leech et al., 2011), more rapidly than at any time in the last 400 years (Chapin III et al., 2004). The associated warmer and drier climatic conditions are expected to change ecosystem structure and increase plant-related environmental stress. Warmer and drier climate conditions are expected to impact ecosystem structure, in certain parts of the world, owing to increased abiotic stress (e.g., wildfire, drought, wind storms, frost, permafrost melting) (Beaulieu and Rainville, 2005; Dale et al., 2001; Haughian et al., 2012). The associated factors leading to increased plant stress include high temperatures and limited water availability. Consequences associated with water stress include decreased germination rates and a reduction in plant hormone levels (including gibberellic acid) owing to a lack of water uptake from the surrounding soils and osmotic stress (Kaur et al., 1998).

Government, industry and environmental service providers are continuously seeking effective, feasible, economic and environmentally sustainable methods to design landscapes and to improve the establishment and growth of desired plant species to achieve reclamation on a faster timeline. Associated benefits include the reduction in environmental and economic liabilities, and a reduction in the costs associated with continued site monitoring and vegetation management.

The production of high quality seedlings from native seed for reclamation has been found to be difficult, owing to poor seed germination and poor root development within plugs; seedling quality will directly impact its survival following out-planting (MacDonald et al., 2015). PGRs may enhance the germination, growth, development, and establishment of native plant seeds and seedlings in greenhouse production of native plant materials as well as during the out-planting of native plant materials within reclaimed and/or reconstructed soils.

2. Types of PGRs

There are five major types of PGRs, including auxins, gibberellins, cytokinins, ethylene, and abscisic acid. Newly identified PGRs including brassinosteroids and jasmonates have also been found to control phytohormonal functions (Rademacher, 2015).

2.1. Auxins

Auxins are low molecular weight organic phytohormones, involved in every aspect of plant growth and development, including the regulation of morphogenesis and stimulation/control of cell division and elongation (George et al., 2008; Saini et al., 2013). Organic and polar in nature, auxins can be transported long distances throughout a plant via plant vascular tissue (George et al., 2008). The literature suggests that auxins are synthesized in both meristematic regions and in growing organs (i.e., leaves, buds, root tips, developing seeds). Concentrations are highest in the leaves, buds and ends of branches, and lowest in the roots. As a result, auxins are most prevalent in younger plants (i.e., seedlings, juveniles) and play a larger role in early stage plant development (George et al., 2008).

Since they are directly affected by light, auxins are responsible for phototropism (growth of a plant in response to light); however, auxins also influence apical dominance, lateral root initiation, vascular development and gravitropism (Davies, 1995; Rademacher, 2015). Auxins have been observed to interact with abscisic acid and salicylic acid to regulate growth during plant adaptation to abiotic stress (Park, 2007).

The addition of natural and/or synthetic auxins to actively growing plants (i.e., foliar application) is thought to improve physiological processes that directly control plant growth. When applied to plant cuttings, auxins can stimulate the formation of roots (Harms and Oplinger, 1988).

Different parts of plants (i.e., shoots, buds, roots) have been found to respond differently to auxins. Therefore, the type and concentration of auxin selected to improve plant growth should depend on the plant species, rate of uptake and transport to target tissue, existing natural levels of auxins within the plant, sensitivity to auxins, metabolic rate, and the interaction between hormones within the plant (George et al., 2008).

Although auxins are necessary for plant survival, high concentrations can lead to negative effects, including oxidative stress, often resulting in cellular death (Flasinski and Hac-Wydro, 2014). Consequently, auxins have been found to act as both stimulators and inhibitors of growth, depending on the concentration applied (Harms and Oplinger, 1988). This finding has led to the development of auxin-derived selective herbicides.

Natural auxins are extracted from a plant or produced by bacteria; natural products are thought to rapidly degrade, limiting the applicability of the product (Reich, 2013). Indole-3-acetic acid (IAA) is the least stable form as it degrades rapidly in light and is susceptible to destruction in plants by the enzyme IAA-oxidase (George et al., 2008). Synthetic auxins are considered to be more effective than natural auxins as they do not oxidize within plant tissue (George et al., 2008). Synthetic auxins are now commercially available in both liquid (dip solutions and post-planting sprays) and powdered forms; liquid forms have been demonstrated to be more rapidly absorbed than powdered forms (Reich, 2013).

2.2. Cytokinins

Cytokinins are phytohormones naturally produced in developing or meristematic tissues and organs (i.e., shoot apex, immature organs, root tips) (Osugi and Sakakibara, 2015; Rademacher, 2015). There are roughly 20 natural plant cytokinins (Therios, 2008). While their specific mode of action remains unknown (George et al., 2008), the effects of cytokinins on plant growth and development are apparent across the literature. Cytokinins are critical for plant cell division, as they directly regulate the synthesis of proteins involved in mitosis. In the absence of cytokinins, the cell cycle has been observed to come to a standstill (George et al., 2008). Cytokinins counteract auxins in apical dominance and promote lateral plant growth, resulting in the production of lateral shoots and roots (Rademacher, 2015). By stimulating cell division, protein synthesis, cell enlargement, senescence and transport of amino acids in plants, cytokinins have been observed to promote shoot generation from internodes, promote maturation of chloroplasts, release buds from dormancy, initiate callus formation and increase the spreading of thick roots (George et al., 2008; Harms and Oplinger, 1988). In addition to promoting root growth, cytokinins also enhance root growth rate (Carrow and Duncan, 2012). As a result, cytokinins play an important role throughout a plant's lifecycle.

Cytokinins have also been found to regulate plant response to light, nutrients, water availability, abiotic stressors and biotic stressors. They